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Benthic assemblages of rock pools in northern Portugal: seasonal and between-pool variability

IACOPO BERTOCCI [1], RITA ARAÚJO [1], MÓNICA INCERA [2], FRANCISCO ARENAS [1], RUI PEREIRA [1], HELENA ABREU [1,3], KIM LARSEN [1] and ISABEL SOUSA-PINTO [1,4]

[1] CIIMAR/CIMAR, Centro Interdisciplinar de Investigação Marinha e Ambiental, Rua dos Bragas, 289, 4050-123, Porto, Portugal. E-mail: ibertocci@ciimar.up.pt
[2] Centro Tecnológico del Mar – Fundación CETMAR, C/Eduardo Cabello, s/n E-36208, Bouzas, Vigo, Spain.
[3] Daithi O'Murchu Marine Research Station, Gearhies-Bantry, Ireland.
[4] Department of Biology, Faculty of Sciences, University of Porto, Rua do Campo Alegre s/n, 4169-007, Porto, Portugal.

SUMMARY: We investigated the seasonal (winter vs summer and within season) and spatial (between-pool) variability of benthic assemblages of rock pools at mid-intertidal level along the shore of Viana do Castelo (North Portugal). Physical traits of rock pools, including size, depth and position along the shore, were also compared between pools. While pools did not differ for any of the examined physical traits, results indicated a clear seasonal difference in the structure of assemblages, including a total of 49 macroalgal and 13 animal taxa. This finding was driven by six taxa that are more abundant in winter (the reef-forming polychaete *Sabellaria alveolata*, the articulated coralline algae *Corallina* spp., the brown alga *Bifurcaria bifurcata*, the encrusting coralline alga *Lithophyllum incrustans*, the red alga *Chondracanthus acicularis* and the grazing snails *Gibbula* spp.) and four algal taxa that are more abundant in summer (the invasive brown *Sargassum muticum*, the green *Ulva* spp., the kelp *Laminaria ochroleuca* and the filamentous red *Ceramium* spp.). These data provide a new contribution to the knowledge of rock pool systems and have potential implications for monitoring programmes aimed at assessing ecological modifications related to natural and anthropogenic disturbances and for identifying processes responsible for the variability of rock pool assemblages.

Keywords: rock pools, rocky intertidal, seasonal variability, benthos, *Sabellaria alveolata*, Portugal.

RESUMEN: COMUNIDADES BENTÓNICAS DE CHARCAS ROCOSAS DEL NORTE DE PORTUGAL: VARIABILIDAD ESTACIONAL Y ENTRE CHARCAS. – Investigamos la variabilidad estacional (invierno vs verano y entre estaciones) y espacial (entre charcas) de las comunidades bentónicas en charcas rocosas del nivel intermareal medio a lo largo de la costa de Viana do Castelo (Norte de Portugal). Además comparamos los parámetros físicos entre las charcas, incluyendo el tamaño, temperatura y posición a lo largo de la costa. Mientras que las charcas no difieren para ninguno de los parámetros físicos examinados, los resultados indican una clara diferencia estacional en la estructura de las comunidades, las cuales incluyen un total de 49 taxones de algas y 13 de animales. Estos resultados fueron inducidos por seis taxones más abundantes en invierno (el poliqueto formador de arrecifes *Sabellaria alveolata*, el alga coralinal articulada *Corallina* spp., el alga parda *Bifurcaria bifurcata*, el alga coralinal incrustante *Litophyllum incrustans*, el alga roja *Chondracanthus acicularis* y los caracoles ramoneadores *Gibbula* spp.) y cuatro taxones de algas más abundantes en verano (el alga parda invasiva *Sargassum muticum*, el alga verde *Ulva* spp., el quelpo *Laminaria ochroleuca* y el alga roja filamentosa *Ceramium* spp.). Estos datos contribuyen al conocimiento de las comunidades de charcas rocosas intermareales y tienen potenciales implicaciones en los programas de monitorización enfocados a medir las modificaciones ecológicas relacionadas con alteraciones naturales y antropogénicas y son útiles para identificar los procesos responsables de la variabilidad de estas comunidades.

Palabras clave: charcas rocosas, intermareal rocoso, variabilidad estacional, bentos, *Sabellaria alveolata*, Portugal.

INTRODUCTION

Investigating patterns of variation in space and time of natural populations and assemblages is a main and challenging goal of ecology (Levin 1992, Underwood *et al.* 2000). Although there is large and widespread evidence that patterns of distribution, abundance and diversity of organisms are heterogeneous over a range

of spatial and temporal scales (Underwood *et al.* 2000, Benedetti-Cecchi 2001, Fraschetti *et al.* 2005, Terlizzi *et al.* 2007, Valdivia *et al.* 2011), this concept is still key for a number of basic and applied ecological issues. As abiotic and biological processes are themselves variable in space and time, examining relevant scales of variation of populations and assemblages is essential to enhance the predictive and explanatory value of ecological models (Andrew and Mapstone 1987, Levin 1992, Underwood and Chapman 1996, Benedetti-Cecchi 2000). Identifying variations of traits of biodiversity over a hierarchy of scales can prevent oversimplified generalizations and clarify how local or current processes can be generalized to larger scales (Underwood and Petraitis 1993, Lawton 1996, Hewitt *et al.* 1998), support assessments of anthropogenic impacts (e.g. Balestri *et al.* 2004) and assist the design of management and conservation measures, including the implementation of marine protected areas (e.g. Benedetti-Cecchi *et al.* 2003). As a consequence, the identification of relevant scales of variation of biological variables has become a legal requirement into management programmes in many countries (e.g. the Water Framework Directive in Europe and the National Environmental Policy Act in the USA).

Tide pools have been reported to be very variable systems at different locations (Metaxas and Scheibling 1993, Metaxas *et al.* 1994, Underwood and Skilleter 1996, Van Tamelen 1996, Thompson *et al.* 2002). Tide pools provide peculiar environmental conditions compared with the surrounding rocky habitats, as they are not subject to the tidal cycles of submersion and desiccation of nearby emergent rocky areas. On the other hand, they experience greater fluctuations of physical variables, including temperature, salinity and pH, compared with subtidal habitats, with the occurrence of very harsh conditions particularly at higher levels on the shore (Metaxas and Scheibling 1993). These factors have been invoked to explain the dominance of different groups of macroalgae in pools located at different tidal levels (Dethier 1982, Wolfe and Harlin 1988a, Kooistra *et al.* 1989, Metaxas *et al.* 1994) and the reduction of species diversity at increasing heights (Femino and Mathieson 1980, Huggett and Griffiths 1986, Wolfe and Harlin 1988b, Kooistra *et al.* 1989). Moreover, assemblages are highly variable between pools located at the same height on the shore (Metaxas and Scheibling 1993, Metaxas *et al.* 1994), probably due to combined abiotic and biological factors. These include physical characteristics, such as size, depth, substratum heterogeneity, orientation and position along the coastline that can provide different microhabitats to different pools (Femino and Mathieson 1980, Metaxas *et al.* 1994), and biotic factors, such as grazing (Chapman 1990, Benedetti-Cecchi and Cinelli 1995) and competition (Van Tamelen 1996, Benedetti-Cecchi 2000), often interacting in complex ways (Astles 1993, Dethier 1984, Benedetti-Cecchi and Cinelli 1996, Masterson *et al.* 2008). This complexity could be responsible for the lower number of studies on patterns of distribution and abundance of assemblages in pools compared with other rocky habitats. However, the great variability of this system suggests a limited possibility to generalize to unstudied sets of rock pools the information previously obtained on patterns and their potential driving processes from other pools.

A few studies have described macroalgal assemblages of rock pools on the Portuguese coast. In this region, each of a number of pools sampled along about 60 km of coast was indicated as being unique in terms of macroalgal assemblages, probably due to biological factors, such as timing of colonization, rather than to physical characteristics of the habitat (Araújo *et al.* 2006). Moreover, Rubal *et al.* (2011) documented seasonal patterns of variability of macroalgal assemblages sampled in pools from two sites between 41°02'N and 41°09'N, although this study did not provide any formal test of differences between pools. As in most previous studies that have focused on algal organisms (but see Metaxas and Scheibling 1993), the benthic animal component of Portuguese rock pool assemblages and patterns of temporal (seasonal and within season) and spatial (among and within pools) variability of sessile assemblages from the present location were not taken into account.

The present study was aimed at comparing temporal and spatial patterns of variation of algal and invertebrate assemblages in rock pools located on the Portuguese coast north of Viana do Castelo. The adopted sampling design allowed us to test hypotheses on differences in the structure of whole assemblages, the abundance of individual taxa and the total number of taxa between summer and winter, between dates within each season and between replicate pools. Physical traits, including size, depth and position along the coast of rock pools, were also measured and tested in order to determine whether their possible variation could have potentially affected differences in the structure of assemblages and in the abundance of individual taxa in pools assigned to each date and season of sampling.

MATERIALS AND METHODS

Study system

The study was carried out between December 2010 and July 2011 in a total of 40 rock pools located along about 1 km of coast north of Viana do Castelo (northern Portugal, between 41°42'01"N and 41°42'16"N). The tidal regime along the Portuguese coast is semidiurnal, with the largest spring tides of about 4 m, and all pools were at a tidal height of 0.5-1 m above Chart Datum. In the study area, the summer and winter season are characterized by clear differences in mean air temperature, mean monthly precipitation, light intensity and period, water temperature and hydrodynamic conditions (see Rubal *et al.* 2011 and references therein for details). Nutrient concentrations are also seasonally variable due to upwelling events that are particularly

intense from April to September (Lemos and Pires 2004). The coast is north-to-south oriented, exposed to prevailing northwest oceanic swell and characterized by a continuous rocky shore with granite as the typical substratum.

At the examined height on the shore, the emergent rock is dominated by the mussel *Mytilus galloprovincialis* (Lamarck) and the barnacle *Chthamalus stellatus* (Poli), while pools host more diversified macroalgal and invertebrate assemblages. Among the most common brown algae are the kelp *Laminaria ochroleuca* Bachelot de la Pylaie, *Bifurcaria bifurcata* R. Ross and the invasive *Sargassum muticum* (Yendo) Fesholt. Red algae typically include *Chondracanthus acicularis* (Roth) Fredericq, *Chondracanthus teedei* (Roth) Kützing, encrusting corallines (e.g. *Lithophyllum incrustans* Philippi), articulated corallines (e.g. *Corallina* spp. and *Jania* spp.) and filamentous species (e.g. *Ceramium* spp.), while common green algae are those of the genus *Ulva*. The reef-forming polychaete *Sabellaria alveolata* Linnaeus is the most common sessile invertebrate, while grazers are mostly represented by snails of the genus *Gibbula*, limpets (*Patella* spp.) and the sea urchin *Paracentrotus lividus* Lamarck.

Sampling design and collection of data

Sampling was repeated on two winter (December 2010 and February 2011) and two summer (June 2011 and July 2011) dates, with an independent set of ten pools assigned at random to each date and interspersed along the study coast. The percentage cover of sessile organisms and the number of individuals of mobile animals were visually estimated in each of three quadrates (30×30 cm) established at random in each pool. Organisms were identified to the most detailed level of taxonomic resolution achievable in the field. Percentage cover estimates were obtained by dividing each quadrate into 25 sub-quadrates of 6×6 cm, assigning to each taxon a score from 0 (absence of that taxon) to 4 (a whole sub-quadrate covered by that taxon) and adding up the 25 estimates (Dethier *et al.* 1993). In each case in which a sessile taxon covered less than one sub-quadrate, an arbitrary value of 1 was assigned. The abundance of organisms attached to both primary and secondary substratum were taken into account. This, in addition to the multilayered structure of assemblages, made the total cover in each quadrate exceed 100% in some cases.

Geographic coordinates of the centre, maximum depth, length, width and size (roughly estimated) were recorded for each pool. The position along the shore was considered relevant due to the south to north orientation of the coastline in the study area and the close presence in the south of the city and port of Viana do Castelo and the estuary of the Lima river. These traits could determine the occurrence of gradients that in theory have different effects on pools located at increasing distances from these sources of physical and chemical disturbance. Pools ranged from 2.5 m to 7.4 m in length, from 1.2 m to 4.8 m in width, from 0.2 m to 0.7 m in depth and from 6.0 m^2 to 33 m^2 in area.

Data analysis

Data were analysed with multivariate and univariate techniques to test the hypothesis that the structure of assemblages, the abundance of individual taxa and the total number of taxa differed between seasons, between dates within seasons and between pools. Preliminary analyses of variance (ANOVA), however, were carried out to test for differences between pools assigned to sampling on each date and in each season in the measured physical variables. Each of these was based on a two-way model, including the factors Season (fixed, with two levels: Winter vs Summer) and Date (random, nested in Season, with two levels), with ten replicates (the ten pools assigned to sampling on each date and in each season).

Permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) based on Bray-Curtis untransformed dissimilarities was used to analyse the multivariate assemblage data. The model for this analysis included the three factors Season, Date (the same as for the previously described ANOVAs) and Pool (random, nested in Season and Date, with ten levels), with three replicates (the three quadrates sampled in each pool on each date). When an excessively low number of possible permutations prevented a test with sufficient power from being obtained, a p-value was calculated using 999 Monte Carlo draws from the appropriate asymptotic permutation distribution (Anderson and Robinson 2003). In order to test whether differences of assemblages between pools, dates and seasons were due to differences in multivariate dispersion between groups rather than mostly in the location of centroids, the same model was tested for differences in dispersion by means of the PERMDISP program (Anderson 2006).

Multivariate patterns were illustrated by non-metric multidimensional scaling (nMDS), involving the calculation of centroids of assemblages for each sampled pool. Principal coordinates were calculated from the Bray-Curtis dissimilarity matrix of the whole set of data and centroids were obtained as averages of the principal coordinates over the three replicates in each pool assigned to each date and season of sampling (McArdle and Anderson 2001). Finally, a matrix of Euclidean distances between each pair of centroids was calculated and used as the input for the nMDS.

The SIMPER procedure (Clarke 1993) was used to determine the percentage contribution (δ_i%) of each taxon to the Bray-Curtis dissimilarity between assemblages sampled in winter and summer (δ_i). A taxon was considered important if its contribution to total percentage dissimilarity was ≥3%. The ratio $\delta_i/SD(\delta_i)$ was used to quantify the consistency of the contribution of a particular taxon to the average dissimilarity in all pairwise comparisons of samples between win-

ter and summer. Values ≥1 indicated a high degree of consistency.

Data on the abundance of relevant (according to the SIMPER results) individual taxa and the total number of identified taxa were analysed with analysis of variance (ANOVA), using the same model as the multivariate case described above.

Before each ANOVA, Cochran's *C* tests were done to check for homogeneity of variances. When possible, data were log-transformed to remove the heterogeneity of variances. When this was not possible, untransformed data were analysed and results were considered robust if not significant (at p>0.05) or significant at p<0.01 (to compensate for the increased probability of type I error, Underwood 1997).

RESULTS

Physical traits

The ANOVA indicated that the ten replicate pools assigned to sampling on each date and in each season did not differ statistically for the position along the shore (season: MS=396.9, $F_{1,2}$=0.03, p>0.8; date: MS=15852.8, $F_{2,36}$=0.26, p>0.7), the depth (season: MS=9.0, $F_{1,2}$=0.20, p>0.6; date: MS=44.4, $F_{2,36}$=0.27, p>0.7 or the size (season: MS=139.3, $F_{1,2}$=1.21, p>0.3; date: MS=115.3, $F_{2,36}$=1.19, p>0.3).

Structure of assemblages

A total of 62 taxa, including 49 macroalgae and 13 invertebrates, were identified. The PERMANOVA analysis revealed significant seasonal differences in the structure of assemblages, not masked by the great variability between dates and between pools (Table 1) and clearly illustrated by the sharp separation of centroids of pools sampled in winter from those of pools sampled in summer (Fig. 1). The PERMDISP analysis, however, indicated that differences between seasons, as well as those between dates and between pools, were actually due to differences in the locations of centroids rather than in their dispersion (F_{Season}=3.36, p=0.09; F_{Date}=0.62, p=0.44; F_{Pool}=1.59, p=0.21).

SIMPER analysis indicated 10 (8 macroalgal and 2 animal) taxa as important (i.e. contributing to ≥3% of percentage dissimilarity) in discriminating between winter and summer. Collectively, these taxa contributed more than 83% to the total dissimilarity (Table 2). The contribution of *Sabellaria alveolata*, *Corallina* spp. and *Ulva* spp. to percentage dissimilarities was highly consistent among pairwise comparisons of samples between the two groups (Table 2).

TABLE 1. – Permutational multivariate analysis of variance (PERMANOVA) on rock pool assemblages. Significant effects are indicated in bold. P(MC)=p-value calculated by Monte Carlo method.

Source of variation	df	MS	pseudo-*F*	p	p(MC)	Permutable units and denominator
Season=S	1	58926.8	6.8	0.315	**0.002**	4 Date(S) cells
Date(S)=D(S)	2	8625.3	2.3	**0.011**		40 Pool(D(S) cells
Pool(D(S))	36	3824.1	3.5	**0.001**		120 Raw units
Residual	80	1097.2				

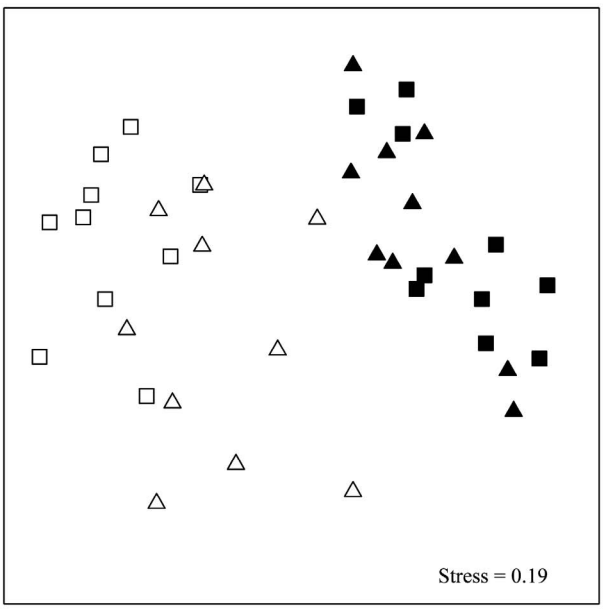

FIG. 1. – nMDS plots of centroids of pools sampled in winter (black) and summer (white), at two dates in each season. Date 1=December 2010 (Winter: full square) and Jun 2011 (Summer: full triangle), Date 2=February 2011 (Winter: open square) and July 2011 (Summer: open triangle).

Individual taxa and total number of taxa

Among the important individual taxa identified by SIMPER, *Sabellaria alveolata* (Fig. 2A), *Corallina* spp. (Fig. 2B), *Bifurcaria bifurcata* (Fig. 2G), *Lithophyllum incrustans* (Fig. 2H), *Chondracanthus acicularis* (Fig. 2I) and *Gibbula* spp. (Fig. 2J) were more abundant in winter than in summer. The opposite pattern between seasons was shown by *Sargassum muticum* (Fig. 2C), *Ulva* spp. (Fig. 2D), *Laminaria ochroleuca* (Fig. 2E) and *Ceramium* spp. (Fig. 2F). The analysis of *S. alveolata*, *S. muticum*, *L. ochroleuca* and

TABLE 2. – Contribution (δ_i) of individual taxa from rock pool assemblages to the average Bray-Curtis dissimilarity between winter (W) and summer (S). Only taxa contributing ≥3% of percentage dissimilarity are included. Values of $\delta_i/SD(\delta_i)\geq 1$ indicate that the contribution of a taxon to percentage dissimilarity was consistent among pairwise comparisons of samples between winter and summer.

Taxon	Average abundance W	S	δ_i	δ_i%	$\delta_i/SD(\delta_i)$
Sabellaria alveolata	36.1	5.0	13.5	17.7	1.1
Corallina spp.	38.3	22.4	11.6	15.2	1.4
Sargassum muticum	7.0	26.5	10.5	13.7	0.9
Ulva spp.	0.4	20.4	9.2	12.0	1.3
Laminaria ochroleuca	3.4	8.5	4.1	5.4	0.7
Ceramium spp.	0.0	8.5	3.9	5.2	0.8
Bifurcaria bifurcata	7.6	1.7	3.4	4.4	0.7
Lithophyllum incrustans	5.8	2.7	2.9	3.7	0.8
Chondracanthus acicularis	4.6	1.7	2.4	3.1	0.7
Gibbula spp.	6.3	2.0	2.2	3.0	0.9

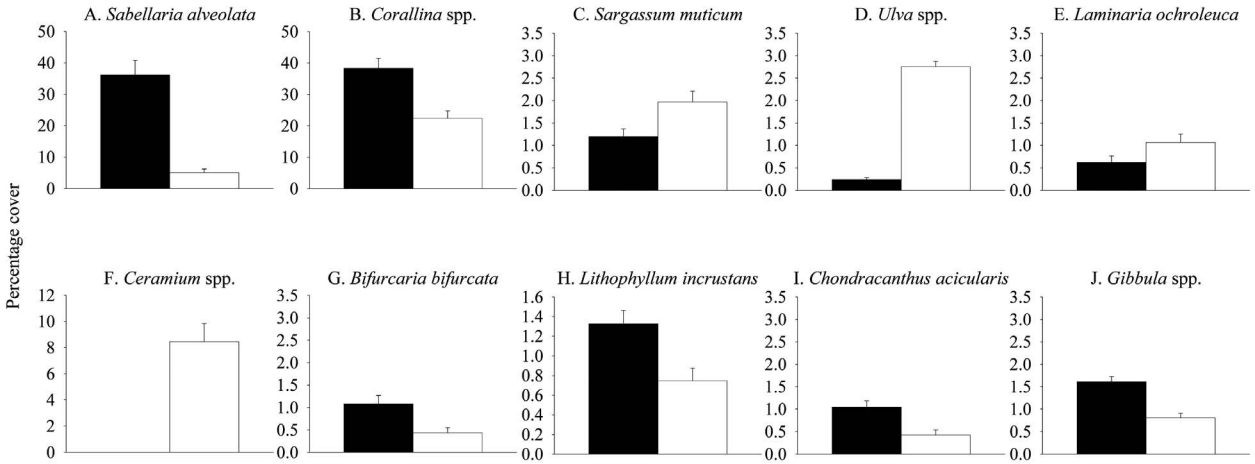

FIG. 2. – Mean (+SE) percentage cover of individual taxa (A, B and F: untransformed data; C, D, E, G, H, I and J: log-transformed data) in winter (black) and summer (white). Data averaged over three replicate quadrates, ten pools and two dates.

TABLE 3. – Summary of ANOVAs for individual taxa from rock pool assemblages. * p<0.05; ** p<0.01, *** p<0.001.

Source of variation	df	*Sabellaria alveolata* MS	*F*	*Corallina* spp. MS	*F*	*Sargassum muticum* MS	*F*	*Ulva* spp. MS	*F*	*Laminaria ochroleuca* MS	*F*	*Ceramium* spp. MS	*F*
Season = S	1	28985.2	6.2	7648.0	90.7*	17.9	1.6	189.8	103.8**	6.0	3.2	2142.1	5.3
Date(S) = D(S)	2	4688.2	3.1	84.3	0.1	11.4	2.6	1.8	2.2	1.8	0.6	407.0	3.3
Pool(D(S))	36	1511.5	6.1***	1049.0	5.0***	4.5	3.0***	0.8	2.8***	2.9	2.6***	125.1	6.8***
Residual	80	249.1		211.5				1.5		0.3	1.1		18.4
Cochran's test		*C*=0.296**		*C*=0.084		*C*=0.119		*C*=0.119		*C*=0.112		*C*=0.321	
Transformation		None		None		Ln(x+1)		Ln(x+1)		Ln(x+1)		None	

TABLE 4. – Summary of ANOVAs for individual taxa and the total number of taxa from rock pool assemblages. * p<0.05; ** p<0.01, *** p<0.001.

Source of variation	df	*Bifurcaria bifurcata* MS	*F*	*Lithophyllum incrustans* MS	*F*	*Chondracanthus acicularis* MS	*F*	*Gibbula* spp. MS	*F*	Total taxa MS	*F*
Season = S	1	12.5	40.5*	10.1	3608.5***	11.6	75.6*	19.4	21.6*	4.0	0.1
Date(S) = D(S)	2	0.3	0.1	0.0	0.0	0.2	0.1	0.9	0.9	75.1	7.3**
Pool(D(S))	36	2.5	2.9***	1.4	1.5	2.0	3.7***	1.1	2.2**	10.3	2.8***
Residual	80	0.9		0.9		0.5		0.5		3.7	
Cochran's test		*C*=0.091		*C*=0.082		*C*=0.151		*C*=0.097		*C*=0.089	
Transformation		Ln(x+1)		Ln(x+1)		Ln(x+1)		Ln(x+1)		None	

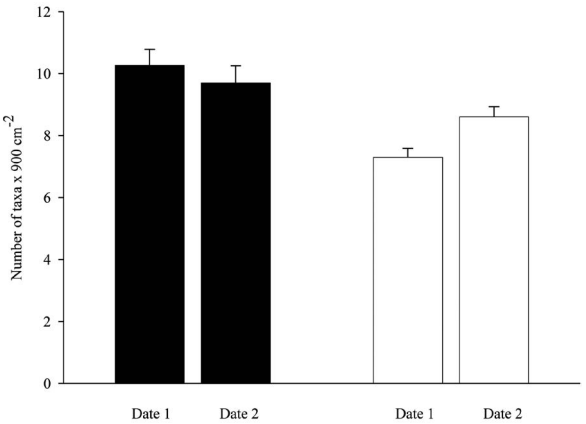

FIG. 3. – Mean (+SE) number of taxa sampled at each of two winter (black) and summer (white) dates. Data averaged over three replicate quadrates and ten pools.

Ceramium spp., however, detected no significant effect of Season, probably due to the low power of the test and the masking effect of the great variability between pools in the abundance of almost all response variables (Tables 3 and 4).

The total number of taxa did not differ between winter and summer, but significant variations were detected between dates within each season (Table 4, Fig. 3). Analogously to all other multivariate and univariate patterns, a large variability between pools was also detected for this response variable (Table 4).

DISCUSSION

The present study documented differences between winter and summer in the structure of algal and invertebrate assemblages. This is in agreement with find-

ings on macroalgal assemblages of rock pools from other locations in the same geographical area (Rubal *et al.* 2011). Here, however, seasonal differences were mainly driven by an invertebrate species, the polychaete *Sabellaria alveolata*, which was more abundant in winter than in summer. This species is responsible for the construction of the largest biogenic reefs in Europe, providing a highly dynamic habitat for diversified associated organisms (Dubois *et al.* 2002, Fournier *et al.* 2010). *Sabellaria alveolata* reefs were indicated as extremely sensitive to the mechanical impact of natural (e.g. storms) or anthropogenic (e.g. trampling) disturbances, which can damage the existing bioconstructions and reduce the density of new recruits (Dubois *et al.* 2002, 2006). On the studied shore, mechanical impacts from waves and trampling have clear seasonal patterns related to the occurrence of extreme storms, mostly in winter (Dias *et al.* 2002) and human frequentation of the shore, which is particularly intense in summer (Araújo *et al.* 2009). As extreme waves could directly cause seasonal differences in the abundance of *S. alveolata* that are opposite to the present patterns and trampling might drastically affect intertidal assemblages on emergent rock rather than in rock pools, both mechanisms are unlikely to provide convincing explanations to our findings. It is worth noting, however, that present bioconstructions of *S. alveolata* are not in the form of reefs, but rather of encrusting colonies adhering to the rock, for whose dynamics other processes might be relevant. Among these, a key role might be played by the availability of sediment in the water column, on which *S. alveolata* depends for its bioconstructions (e.g. Desroy *et al.* 2011). No data on sediments were collected in the present study, but it could be logically assumed that the greater intensity of precipitations in winter (Dias *et al.* 2002) might cause a larger input of terrigenous sediments on the shore. This input might have caused favourable conditions for the development of larger covers of encrusting *S. alveolata* in winter than in summer. In summer, instead, the established colonies could have suffered the negative effects of even relatively mild disturbances, such as waves and trampling, not counteracted by large amounts of available sediments. Alternatively, but not mutually exclusively, seasonal patterns in the abundance of *S. alveolata* could have been driven by differential hydrodynamic patterns affecting the distribution of larvae of this species in the water and their possibilities of settling. Laboratory studies have indicated that the larval life of *S. alveolata* can last several months (Wilson 1970). Although this period is likely shorter under natural conditions and spawning of *S. alveolata* in the NE Atlantic has been indicated to occur mostly between April and October (e.g. Dubois *et al.* 2007), planktonic larvae of this species could have been present in the study area in both winter and summer. During winter months, the main currents on the Portuguese coast flow northward, while a prevailing flow in the opposite direction occurs during the summer (Coelho *et al.* 2002, Huthance *et al.* 2002). We cannot hypothesize how this hydrodynamic process could have worked in detail, but in principle it might have caused a larger transportation of larvae, and thus a larger settlement and development of *S. alveolata* colonies, from southern locations where this species is particularly abundant (e,g, the Belinho area located about 10 km apart from the study site, unpublished data) to rock pools in winter than in summer. Laboratory studies (e.g. Ayata *et al.* 2009) have indicated that the hydrodynamic regime is essential for the success of dispersal and settlement of larvae and for the growth of adults of *S. alveolata*, probably by affecting connectivity among populations (Caley *et al.* 1996) or through the transportation of sediments with a grain size and shape that are more suitable for their bioconstructions (Godet *et al.* 2011).

Articulated algae of the genus *Corallina* were also more abundant in pools sampled in winter than in summer. Drastic reductions of intertidal populations of *Corallina elongata* during summer months were documented in the Strait of Gibraltar (Guerra-García *et al.* 2011), and peaks in abundance during late autumn-winter were shown by geniculate coralline algae in rock pools from the Azores (Neto 2000) and the NW Mediterranean Sea (Benedetti-Cecchi and Cinelli 1994). These seasonal fluctuations could be explained by the sensitivity of these algae to stressful environmental conditions occurring during summer, including high temperatures and osmotic stress (Davison and Pearson 1996, Guerra-García *et al.* 2010), while their calcified thallus is able to resist under strong wave action and abrasion, typically occurring during the winter (Littler and Kauker 1984). In addition, articulated coralline algae can regenerate quickly from their persistent basal crust (Littler and Kauker 1984, Konar and Foster 1992), a trait that could have favoured them over potentially better competitors in disturbed patches created by winter storms (e.g. Benedetti-Cecchi *et al.* 1996).

Although with less overall covers, other macroalgal species with very different life histories showed greater abundances in winter than in summer. For the brown *Bifurcaria bifurcata* and the red *Chondracanthus acicularis*, a possible explanation could involve the negative effect of competing species. It has been indicated, for instance, that the abundance of *B. bifurcata* is drastically reduced in the presence of large covers of the invasive seaweed *Sargassum muticum* (Viejo 1997, Sánchez *et al.* 2005), most likely due to the light reduction occurring under the *S. muticum* canopy (Britton-Simmons 2004), while negative effects of this invader on native macroalgae could be negligible when its abundance is low (Arenas and Fernández 2000, Sánchez and Fernández 2005). The increase in abundance of *S. muticum* in summer compared with winter might therefore have played a role in maintaining corresponding variations in the abundance of the native *B. bifurcata* and *C. acicularis* in our rock pools. Further support to this model could come from the observation that increases in cover of northeast Atlantic

C. acicularis populations are likely due to vegetative propagation (Guiry and Cunningham 1984), a process whose success would be inversely related to the preemption of the substratum by *S. muticum*. Interactions of abiotic and biological factors, instead, might explain seasonal patterns of *Lithophyllum incrustans*. Encrusting coralline algae were described as poor competitors for space (Breitburg 1984), but their morphology and life traits make them very resistant to physical disturbance. They thus tend to dominate in rocky habitats exposed to severe abiotic stress, including the mechanical impact of waves (e.g. Bertocci *et al.* 2005), and to intense grazing that can remove potential algal competitors (Steneck 1986, Airoldi 2000, Bulleri *et al.* 2002). As stated above, such favourable abiotic conditions, normally occurring at the study site during the winter might have contributed to present findings on *L. incrustans*. Further supporting seasonal variations in the abundance of grazers, such as limpets and sea urchins (e.g. Bulleri *et al.* 2002 and references therein), usually responsible for the maintenance of barren habitats dominated by encrusting corallines, were not found in the present study. The greater abundance of grazing gastropods *Gibbula* spp. sampled in winter than in summer and the opposite pattern of ephemeral algae such as *Ulva* spp. and *Ceramium* spp., however, were consistent with this model. On the other hand, it is unlikely that the larger cover of *L. incrustans* during the winter was just the result of some sampling artefact due to the reduced secondary cover of canopy-forming species, such as *Sargassum muticum* and *Laminaria ochroleuca*, allowing a better estimation of understory encrusting organisms. The low cover of these species (7% and 3.4% on average, respectively) prevented the occurrence of such a mechanism.

According to previous findings, environmental factors such as light (Cheshire *et al.* 1996, Golléty *et al.* 2008) and nutrient availability (e.g. Masterson *et al.* 2008) can directly control the productivity of several intertidal algae and of *Ulva* spp. in particular. Solar irradiation and concentrations of nutrients in the water due to upwelling events were reported as greater in summer than in winter months in the study area (Lemos and Pires 2004). Under such conditions, adding to their large ability to reproduce and propagate through spores, zygotes and vegetative fragments (Burrows 1991), species of the genus *Ulva* may have quickly reached their maximum abundances, occupying the substratum to the detriment of other algal species (e.g. Guimaraens and Coutinho 2000). The availability of nutrients, adding to reduced pressure by grazers, could also explain the presence of *Ceramium* spp. in summer samples only, as there is evidence that these species can increase in abundance when grazing control is relaxed (Masterson *et al.* 2008) and can become P-limited in the periods of the year when the water concentration of nutrients is lower (Pedersen *et al.* 2010).

Present seasonal variations in the abundance of *S. muticum* are consistent with previous observations of its fast spring growth, early summer reproduction and late summer senescence (Arenas *et al.* 1995, Arenas and Fernández 2000). Although this species can dominate rock pool assemblages throughout the year (e.g. Baer and Stengel 2010), a key factor driving this seasonal pattern seems to be intraspecific competition under crowded conditions, such as in periods of fast growth (Arenas and Fernández 2000, Arenas *et al.* 2002; Steen 2003).

The greater abundance of the perennial kelp species *Laminaria ochroleuca* in summer than in winter can be interpreted mainly as a result of seasonal changes in abiotic variables, primarily the temperature. In fact, *L. ochroleuca* is considered the only warm-temperate species within the digitate group of the genus *Laminaria* (tom Dieck 1992) and it has been indicated that its maximum percentages of germination, reproductive success and growth rates occur under ranges of temperature corresponding to those documented for the summer period in the study area (Izquierdo *et al.* 2002, Rubal *et al.* 2011). Conversely, its failure in reproduction and drastically reduced growth at temperatures around 10°C would make this species less competitive in winter (Izquierdo *et al.* 2002).

Finally, although unable to mask differences between seasons, present findings indicated a large variability between pools in the structure of assemblages, analogously to previous studies (Metaxas *et al.* 1994, Araújo *et al.* 2006). Such variability is often attributed to physical characteristics of each pool. Here, however, spatial and temporal differences were unlikely to be affected by physical traits that are usually considered as particularly important, such as size, depth and position (Femino and Mathieson 1980, Wolfe and Harlin 1988b, Metaxas *et al.* 1994, Araújo *et al.* 2006), as these were comparable between pools assigned to each date and season. Other single or interacting abiotic and biological factors, such as the heterogeneity of the substratum, grazing and patchy algal recruitment and colonization, could thus make a larger contribution to driving the variability of assemblages between pools (Menge *et al.* 1983, Reed *et al.* 1988, Benedetti-Cecchi and Cinelli 1992, 1995).

The present documentation of the importance of invertebrate taxa and of seasonal and between-pool patterns of distribution of assemblages from areas where such issues had never been addressed before adds new data to the knowledge of the great variability of rock pool systems, with important implications. First, when integrated into longer-term and larger-scale monitoring programmes of coastal assemblages, such data can help to identify ecological modifications related to natural and anthropogenic disturbances (Roberts *et al.* 1998, Díez *et al.* 2009). Second, they provide a required basis for identifying and testing the effects of processes responsible for the great variability of assemblages in these rock pools, as even generalizations of findings from apparently similar or nearby systems would be difficult.

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